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Heteromorphism in *Helianthemum*

BY JOHN HENDLEY BARNHART

It is no new discovery that in some of our common North American species of *Helianthemum* the flowers are of different forms on the same plant. In 1824, Dunal, in the first volume of DeCandolle's *Prodromus*, described 112 species of *Helianthemum* known to him; only seven of them were American, and of these he constituted the section *Lechioides*, but no mention is made of the occurrence of heteromorphism. In the same year, however, Elliott (*Bot. S. C. & Ga.* 2: 5), at the end of his description of *H. corymbosum*, remarks: "Frequently in a corymb, one or two flowers rise conspicuously above the rest, and the capsules then become much larger."

Sweet's great illustrated work on the Cistineae was published in parts from 1825 to 1830, and it is easy to trace through its pages the development of the author's ideas about heteromorphism in the American species of *Helianthemum*. Under No. 11, *H. polygalaefolium*, published in November, 1825, he says: "we have not seen any perfect flowers of *H. Brasiliense*, as it did not bloom till autumn, and the flowers were all apetalous, which was also the case with the autumn flowers of the present species, and all the other species of this section that we have had an opportunity of examining this season; the apetalous flowers all produce perfect seeds, but we cannot understand the reason of their producing perfect flowers only in summer."

Under No. 21, *H. Canadense* (May, 1826): "Its handsome flowers are produced in abundance in July and August; after that time it continues to bloom and ripen seeds plentifully until October; but the flowers after August are all without petals, the calyx and capsules are also smaller and of a different form from those produced by the flowers with petals; this is also the case with *H. polygalaefolium* and *Brasiliense*, and we expect with the whole of this section." Under No. 43, *H. Brasiliense* (March, 1827): "the present drawing was taken last May, the first time that it produced perfect flowers; those that were produced the preceding autumn

being all apetalous, as are the autumn flowers of all the species of this section that we have had an opportunity of seeing; but those apetalous flowers produce as perfect seeds as the complete flowers."

Under No. 99, *H. Carolinianum* (July, 1829), no mention of heteromorphism is made, although it is placed in the section *Lechioides*; yet under No. 110, *H. glomeratum* (January, 1830), is given the following broad generalization: "Like all the other American species that we have yet seen or heard of, it belongs to the section *Lechioides* of DeCandolle; all the species of which produce flowers with petals, in the spring and early in summer, whereas all those that are produced in autumn, which are much more numerous, are all apetalous."

Spach (Ann. Sci. Nat. II. 6: 370. D. 1836) segregates all the American species formerly referred to *Helianthemum*, except *H. Carolinianum*, in a new genus *Heteromeris*, characterized by the two kinds of flowers on each plant; Torrey and Gray (Fl. N. Am. 1: 151. 1838) correctly attribute heteromorphous flowers to all their North American species except *H. scoparium* and *H. Carolinianum*; and the investigation here reported shows that of all the species since described from the same territory (California excepted) none is truly homomorphous.

My attention was first called to this subject by finding an apparently undescribed species of *Helianthemum* in Florida, which upon examination proved referable to the heteromorphic group. Yet its affinity was evidently with *H. Nashii*, which was originally described as having the flowers all alike, and this led to a careful reëxamination, first of the available material of *H. Nashii*, and then of the other North American species.

The most recent review of our species is to be found in Gray's Synoptical Flora (1¹: 189-191. 1895) where four species, *H. Canadense*, *H. majus*, *H. capitatum* and *H. corymbosum*, are said to have heteromorphous flowers, while five, *H. arenicola*, *H. Nashii*, *H. Carolinianum*, *H. scoparium* and *H. Greenei*, are described with the flowers homomorphous. *H. arenicola* and *H. Nashii* must have been placed among the homomorphous species merely because of their original descriptions. Since the appearance of the portion of the Synoptical Flora here referred to, an excellent new species (*H. Georgianum*) has been added (Chapman, Fl. So. U. S.

Ed. 3, 36. 1897); and this, too, contrary to its original description, proves upon careful examination of authentic material to have heteromorphous flowers.

In certain respects the heteromorphism varies in different species. In *H. Canadense* and *H. majus* the petaliferous flowers appear in spring, and are solitary, while the apetalous flowers are autumnal and in clusters; in the remaining species, however, the petaliferous and apetalous flowers appear together, in the same clusters and at about the same time. In *H. Canadense*, *H. majus* and *H. capitatum*, the calyx of the complete flower is much larger than that of the incomplete one; in *H. corymbosum* the contrast is much less striking; while in *H. Georgianum*, *H. arenicola* and *H. Nashii* there is practically no difference in the size of the calyx in the two kinds of flowers. This probably accounts, at least in part, for the fact that heteromorphism has never been suspected in the last three species. The complete flowers are always on longer pedicels than the incomplete ones, in some species many times longer. Flowers intermediate in various degrees between those with perfect expanding petals, and those with no petals whatever, are occasionally present in some (perhaps all) of the species.

Besides the features already noted, which may be seen at a glance—the presence or absence of petals, the size of the calyx, and the length of the pedicels—there are certain less conspicuous but more important differences. In the complete flowers the stamens are from 12 to 30 in number, and the filaments far exceed in length the ovary and even the calyx; the style is very short but distinct, and the ovules are usually numerous (20–60, only 8–10 in *H. capitatum* and *H. Nashii*). The incomplete flowers are cleistogamous, and fertilized very early in the bud; in them the stamens are always less numerous than in the complete ones (only 3–8), the filaments just enough shorter than the ovary, so that the anthers are in contact with the stigma; this rests upon the summit of the ovary, but as it is large, and is contracted to a small point of union with the ovary, it is more exact to say “style obsolete” than “stigma sessile”; and the ovules are always fewer than in the complete flowers of the same species, as a rule less than half the number (6–20, only 3–6 in *H. capitatum* and *H. Nashii*). Of course, the seeds are more numerous in the

individual capsules from the petaliferous flower than in those from the apetalous flowers, but it is unusual for all the ovules to mature in either case.

Following is a table showing the number of stamens and ovules in each kind of flower in each of the species under discussion. The material studied, in addition to my own herbarium, is in the herbaria of the New York Botanical Garden and Columbia University. The table is the result of numerous careful dissections, but all the species are not equally well represented, so that in some instances these figures might be slightly altered by a further study of better material.

	Petaliferous Flowers.		Apetalous Flowers.	
	Stamens.	Ovules.	Stamens.	Ovules.
<i>H. Canadense.</i>	30	30-60	4	6-20
<i>H. majus.</i>	30	30-60	4	6-20
<i>H. capitatum.</i>	12-20	8	3	3
<i>H. Nashii.</i>	15	8-10	5	3-6
<i>H. arenicola.</i>	25	20	5	10
<i>H. corymbosum.</i>	25-30	20	3-6	9
<i>H. Georgianum.</i>	12-16	35	8	17

An examination of the available material of the remaining North American species (including the Mexican ones) shows that *H. glomeratum*, *H. argenteum* and *H. Chihuahuense* are heteromorphous, while *H. scoparium*, *H. Greenei*, *H. Mendocinense*, *H. nutans*, *H. patens*, and *H. Pringlei* seem to form quite a natural group, with homomorphous flowers. *H. Carolinianum* is also homomorphous, but otherwise shows a much closer relationship with the heteromorphous species than with the group just referred to. In fact, it seems to me like a heteromorphous species which has lost its apetalous form of flowers; and it would not surprise me, if its origin could be traced, to find that it had heteromorphous ancestors.

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